

NYMPHS OF PALAEODICTYOPTERA (INSECTA) FROM THE WESTPHALIAN OF ENGLAND

by ROBIN J. WOOTTON

ABSTRACT. The remains of three nymphal Palaeodictyoptera from the English Coal Measures (Upper Carboniferous) are described: *Rochdalia parkeri* Woodward 1913; *Idoptilus onisciformis* n. gen., n. sp.; and a wing pad and prothoracic fragment situated in the pelvis of the holotype of the amphibian *Eugyrinus wildi*. The two named nymphs are onisciform, with prothoracic and true abdominal paranotal lobes, and posterolaterally directed wing pads; they show no aquatic adaptations; and the relief of their pronota is complex, and comparable with that of the meso- and metanota. The fossils are not assigned to families; but *Idoptilus* is compared with Eugereonidae and Breyeriidae, and *Rochdalia* and the third nymph with Dictyoneuridae. The prothoracic paranota and wing pads may have been capable of movement.

IN the course of work for the Treatise on Invertebrate Palaeontology, Dr. W. D. I. Rolfe discovered that *Rochdalia parkeri* Woodward 1913, from the Lower Coal Measures of Lancashire, previously supposed to be a branchiopod crustacean, was really an insect nymph. In 1967 he published illustrations and a brief account of *Rochdalia*, and of a similar nymph from the Middle Coal Measures of Barnsley, Yorkshire (British Museum (Natural History) In 44654), suggesting that both might belong to the extinct Order Palaeodictyoptera. He then most courteously invited me to undertake their formal description.

Dr. Rolfe's discovery was of particular interest, as in 1967 no authentic juvenile stages of the extinct palaeopterous insect orders had been properly described as such. At about that time, however, several relevant fossils were in process of study: nymphal Megasecoptera and a palaeodictyopterous nymph from the Upper Carboniferous of Illinois; mayfly nymphs from the Lower Permian of Czechoslovakia and Kansas; and nymphal and adult Palaeodictyoptera from the Upper Carboniferous of Siberia. Moreover Dr. Kukulová was revising the Stephanian Palaeodictyoptera of Commeny, France, and it was evident that this work would greatly clarify the structure and classification of the Order. It seemed sensible, therefore, to delay publishing the account of the English nymphs until some of this material was in print; the more so since doubt was expressed (Carpenter and Richardson 1968) as to whether these insects were indeed Palaeodictyoptera.

The new work (Carpenter and Richardson 1968; Kukulová 1968, 1969*a*, *b*, 1970; Sharov 1971) has in fact helped to confirm the position of *Rochdalia* and the Barnsley nymph in the Palaeodictyoptera. Their description follows; and the opportunity is taken to describe a wing pad and part of the thorax of another nymph, also apparently palaeodictyopterous, which is located in the pelvis of the holotype of the amphibian *Eugyrinus wildi* (Woodward 1891) from the Lower Coal Measures of Lancashire. This latter specimen is considered too fragmentary to merit formal naming. The Barnsley nymph is named, however, as its completeness and preservation are comparable with those of *Rochdalia*.

SYSTEMATIC DESCRIPTIONS

Order PALAEODICTYOPTERA

Family *incertae sedis*

Genus ROCHDALIA Woodward 1913

A partial synonymy was given by Rolfe (1967). The generic characters are at present indistinguishable from those of the type species.

Type species. Rochdalia parkeri Woodward 1913.

Rochdalia parkeri Woodward 1913

Plate 132, figs. 1-2; text-fig. 1

Holotype. L 11464, Manchester Museum: the obverse and reverse impressions of a nymph, situated in an ironstone nodule from above Arley Mine Seam, *communis* Zone, Lower Coal Measures, Sparth Bottoms, Rochdale, Lancashire.

Description. The specimen lacks most head appendages, legs, the distal parts of the cerci, and much of the left side. Only the dorsal aspect is visible.

Length, excluding cerci: 22 mm. Reconstructed width of third abdominal segment, including paranota: 10 mm.

Head: relatively broad (3.5 mm); apparently preserved in hypognathous position; with an anterior median lobe. Eyes small, prominent, widely spaced. No clypeus visible. Anteriorly, the basal parts of two appendages can be seen diverging on either side of the slight anterior lobe of the head. These show no segmentation; they may be the maxillary palps.

Thorax: prothorax, mesothorax and metathorax approximately equal in length, and showing a median keel which is continued on the abdominal nota. Pronotum bearing paranotal lobes, anteriorly arising high on the notum, close to the mid-line, but continuous posteriorly with the hind margin of the notum. Paranota rounded-triangular; the hind margin more or less perpendicular to the longitudinal body-axis, the fore margin running anteromesally to a rounded peak, level with the front of the head, thence posteromesally in an oblique concave arc. Three straight veins diverge from a point near the base of the paranota, about two thirds of the distance from the anterior peak to the posterior margin. The pronotum extends anteriorly beyond the insertion of the paranota as a plate, laterally emarginated, which overlies the back of the head. Behind the plate, the pronotum shows considerable relief, which seems similar in detail to that on the other thoracic nota; although on a smaller scale, being confined to the relatively narrow region between the paranota. Detailed description and interpretation of the thoracic relief must await later study, including reference to adult insects.

Mesothorax and metathorax are similar, being emarginated posteriorly, and about as broad as they are long. The relief appears to show scutal and scutellar regions, together with a broad posterior band which is continuous with the anal region of the wing pads.

The wing pads are directed posterolaterally, and are broadly attached to the terga, there being a wide trough in the area of junction. The mesothoracic pad has a broad

costal area, making the outer margin of the pad nearly parallel to the body axis, and bringing it into alignment with the outer edge of the prothoracic paranotum. The costal margin of the metathoracic pad is more curved, and the costal area narrower than in the mesothoracic pad. The pads are equal in length (7 mm), and, behind Sc, in breadth (c. 3 mm). Venation is poorly preserved and seems similar, if not identical, in the two pads. Sc and R₁ are long and more or less parallel. Parts of Rs and M may be seen in both pads, and CuA in the hind pad only.

Abdomen: tapering towards the rear, with ten recognizable terga. The posterior margin of each is concave; the degree of concavity increasing from segments 2–9. Segment 1 is laterally obscured by the metathoracic wing pad. The remaining segments each bear a pointed posterolaterally directed paranotal lobe, slightly raised above the plane of the tergum. The lobes appear to be in homologous series with the prothoracic paranotum and the wing pads. Each lobe shows a slight ridge, with a groove behind, nearly parallel to the anterior margin, and which appears to correspond in position with the anterior margin of the lobe of the succeeding segment where it underlies its predecessor. On each tergum, too, a line is visible which seems to represent the position of the front edge of the tergum succeeding; suggesting that each overlapped the one behind to a marked degree. Near this line, and about two thirds of the distance from the keel to the origins of the paranota, there is visible on each side of each segment a shallow depression, whose function is not apparent.

Segment 10 bears two broad cerci, of which c. 5 mm are preserved.

Affinity. In our present ignorance it would have been hard to identify *Rochdalia* conclusively as a palaeodictyopteran were it not for the Barnsley nymph, whose better preserved venation places it assuredly in this Order; and which *Rochdalia* closely resembles. *Rochdalia*, however, displays some characters more clearly than the Barnsley nymph, and these support its allocation to the Palaeodictyoptera. They are as follows.

1. The form of the prothoracic paranota. Prothoracic paranota which there is good reason to believe to be primary structures homologous with the wings occur in two insect groups: the Order Palaeodictyoptera: and in some members of the complex of primitive neopterous forms grouped by Carpenter (1966) in the Protorthoptera, and by Sharov (1968) in the Protoblattodea. The pronotal shield of the related Blattodea may also be homologous, in part at least, with the primary paranota.

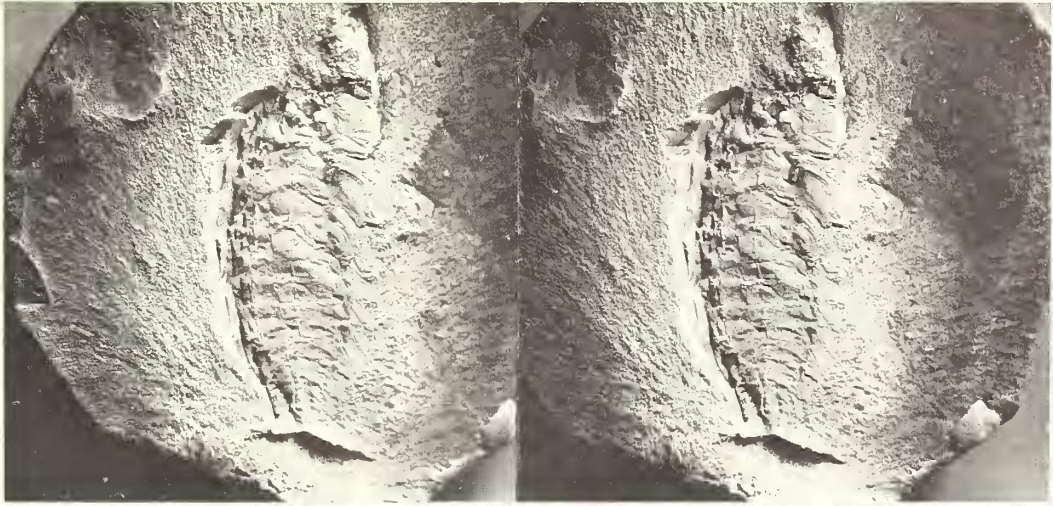
Only in Palaeodictyoptera and in the protorthopterous Lemmatophoridae are paranota known to occur as two large separate lobes, set high on either side of the pronotum. In *Rochdalia* the lobes appear to arise in this position anteriorly; but they are broadly attached, and their posterior margin is continuous with that of the pronotum. The hind edges of the wing pads, however, are also continuous with their respective segments, and it is probable that this is in both cases a condition of the nymph, and that the paranota of the adults had narrow bases, like the wings.

EXPLANATION OF PLATE 132

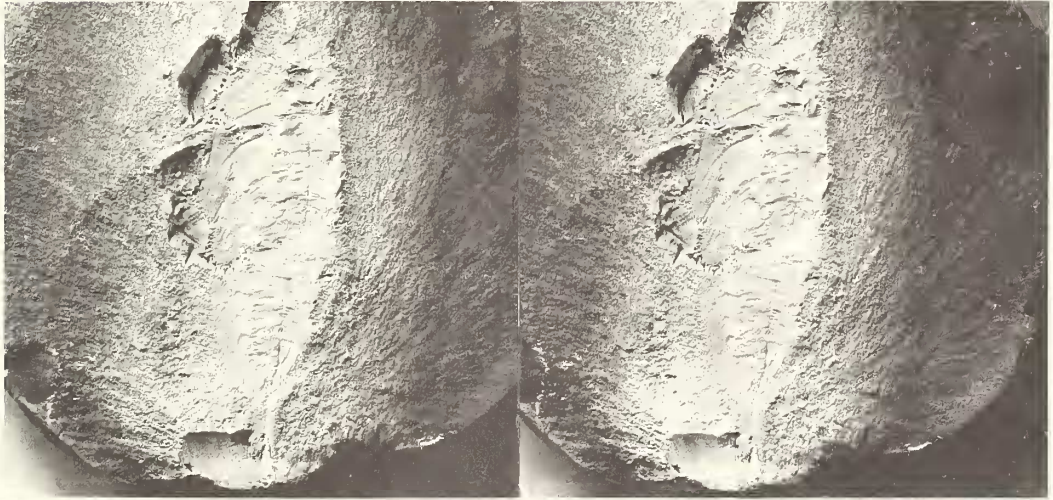
Figs. 1, 2. *Rochdalia parkeri*, Stereoscopic photographs. Specimens whitened with ammonium chloride.

1, Convex impression, $\times 2$. 2, Concave impression, $\times 2$.

Fig. 3. *Idoptilus onisciformis*, convex impression, $\times 1.5$. Stereoscopic photograph. Specimen whitened with ammonium chloride.



1



2



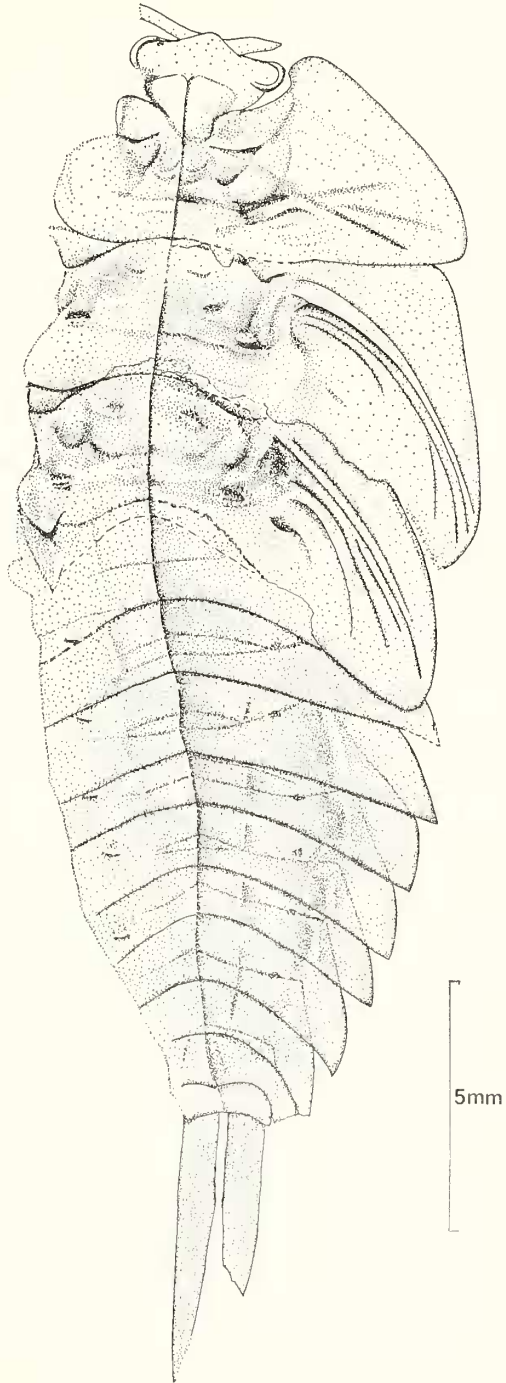
3

The anterior peak of the paranota is odd, and nothing similar is known in adult Palaeodictyoptera. Paranota extending forward on either side of the head do, though, occur in this Order; most notably, perhaps, in the Dictyoneuridae (Kukalová 1970, figs. 50, 55). The head of *Rochdalia*, however, appears rather broad for this family.

Rather similar paranota occur on the undescribed nymph of uncertain affinity (Hunterian Museum, Glasgow University A 2680a) from the same horizon and locality as *Idoptilus onisciformis*, figured by Rolfe (1967, pl. 50, fig. 8; text-fig. 2a). This nymph too is onisciform; as is *Euryptilodes horridus* Sharov 1961, placed by that author in the Protoblattodea, from the L. Permian of the Kuznetsk Basin, Siberia. Both show superficial overall resemblance to *Rochdalia* and *Idoptilus*, which may be convergent.

2. The abdominal paranota. These are known in few adult Palaeodictyoptera, but are arguably present in the Dictyoneuridae. Kukalová (1970) has denied that the lateral abdominal structures in *Stenodictya* are true paranota, homologous with those of the prothorax; and this will be discussed later. It is worth noting here that the form and relationships in *Rochdalia* and in Dr. Kukalová's figures of *Stenodictya* appear very similar, when allowance has been made for the post-mortem distension of the *Stenodictya* abdomens; and furthermore that both show oblique ridges running to the apices of the lobes, which seem to mark the position of the underlying anterior edges of the nota following.

3. The cerci. Strong filiform cerci are widespread in Palaeodictyoptera. They also, however, occur in Ephemeroptera,



TEXT-FIG. 1. *Rochdalia parkeri* Woodward, Manchester Museum L.11464, $\times 6.6$. Drawn by tracing photographs taken both by oblique light and with the specimens immersed in alcoholic glycerin. The drawing is based on the convex impression, but includes details, particularly of the head and wing pads, derived from the counterpart.

Megaseoptera, Diaphanopteroidea, Archodonata and Plecoptera, and were probably present in many Protorthoptera.

Further, but entirely inconclusive suggestions of dictyoneurid affinity come from the apparent homonymy of the fore and hind wings; and from the posterior emargination of the abdominal tergites, which is far more marked in adult *Stenodictya* abdomens than in those of other known Palaeodictyoptera. Homonomous fore and hind wings occur, however, in many palaeodictyopterous families, and the structure of the abdomen is known in few. It is therefore impossible confidently to assign *Rochdalia* to any family; the more so since one cannot be certain how many characters are nymphal adaptations absent from the adult.

Genus *IDOPTILUS* gen. nov.

The generic characters are at present indistinguishable from those of the type species.

Type species. Idoptilus onisciformis sp. nov.

Derivation of name. Idos—needle; *ptilon*—wing.

Idoptilus onisciformis sp. nov.

Plate 132, fig. 3; text-figs. 2, 3A, 3B

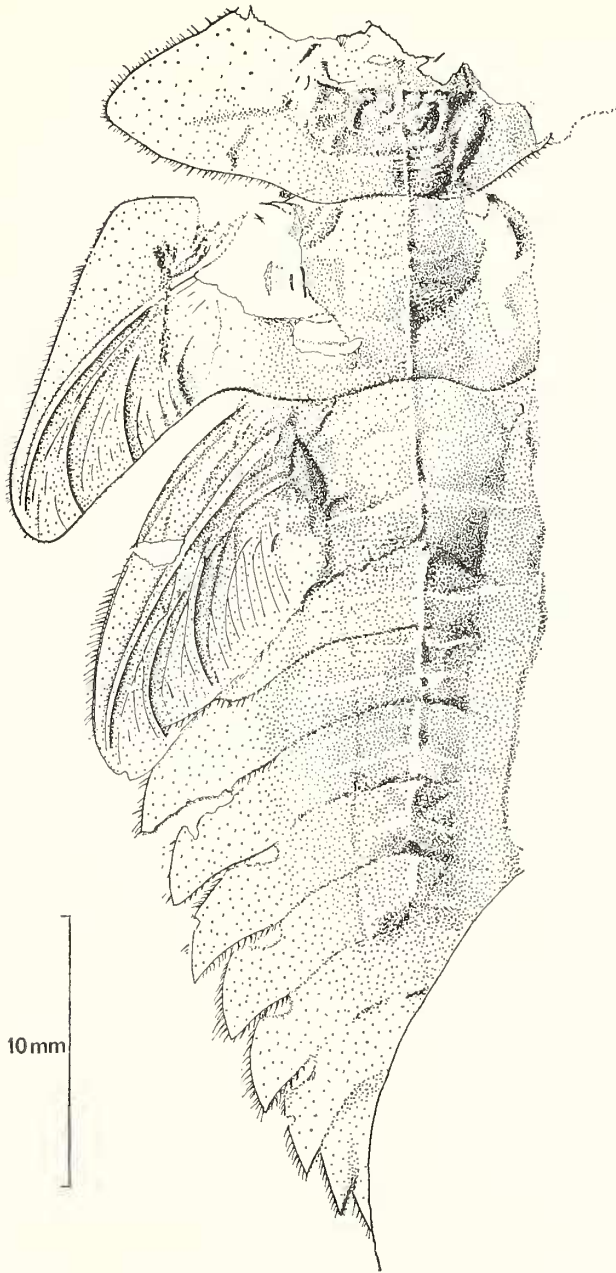
1967 'Rochdalia-like nymph', Rolfe, pp. 310–311, pl. 50, figs. 5–7, text-fig. 2B

Holotype: In 44654, British Museum (Natural History), the dorsal aspect of a nymph in an ironstone nodule from above the Barnsley Coal, *similis-pulchra* Zone, Middle Coal Measures. Round Green open cast mine, Barnsley, Yorkshire.

Description. The specimen lacks the head, appendages, anterior margin of the pronotum, most of abdominal segments 7–9, segment 10, and much of the right side of the entire body. Some traces of the cuticle remain, particularly along the margins of the wing pads and paranota, which are fringed throughout with short spines. The surface of the insect is covered with papillae, which are much coarser on the terga than on the wings or paranota.

Length of specimen 45 mm. Reconstructed width of second abdominal segment including paranota 20 mm.

Thorax: Prothorax, mesothorax and metathorax approximately equal in length, and showing a median keel which is continued on the abdominal terga at least as far as segment 5. Pronotum bearing large triangular paranotal lobes marked off from the notum by a wide, crescent-shaped furrow. The anterior edge of the lobe lies at *c.* 65°, the posterior at *c.* 110° to the longitudinal body axis. Venation of paranotum obscure, but a single vein-like groove, nearly perpendicular to the body axis, appears to give rise at about one third of its length to two oblique branches running respectively anterolaterally and posterolaterally. The pronotum shows considerable relief which, as in *Rochdalia*, appears comparable to, though smaller than that on the meso- and metanota. Mesothorax and metathorax about as broad as long, and similar in size and detail. The posterior margin of the mesonotum is slightly emarginated; that of the metanotum is not preserved. The relief is marked, and as in *Rochdalia* appears to show scutal and scutellar regions and a broad posterior band. Both segments bear large posterolaterally



TEXT-FIG. 2. *Idoptilus onisciformis* n. gen., n. sp. British Museum (Natural History)
In 44654, $\times 3.6$. Drawn by tracing photographs taken by oblique light.

directed wing pads, marked off from the notum by broad grooves; that of the meta-thorax being particularly deep. The area of junction between the mesonotum and its pad is partly destroyed, and the pad appears slightly displaced from its proper position.

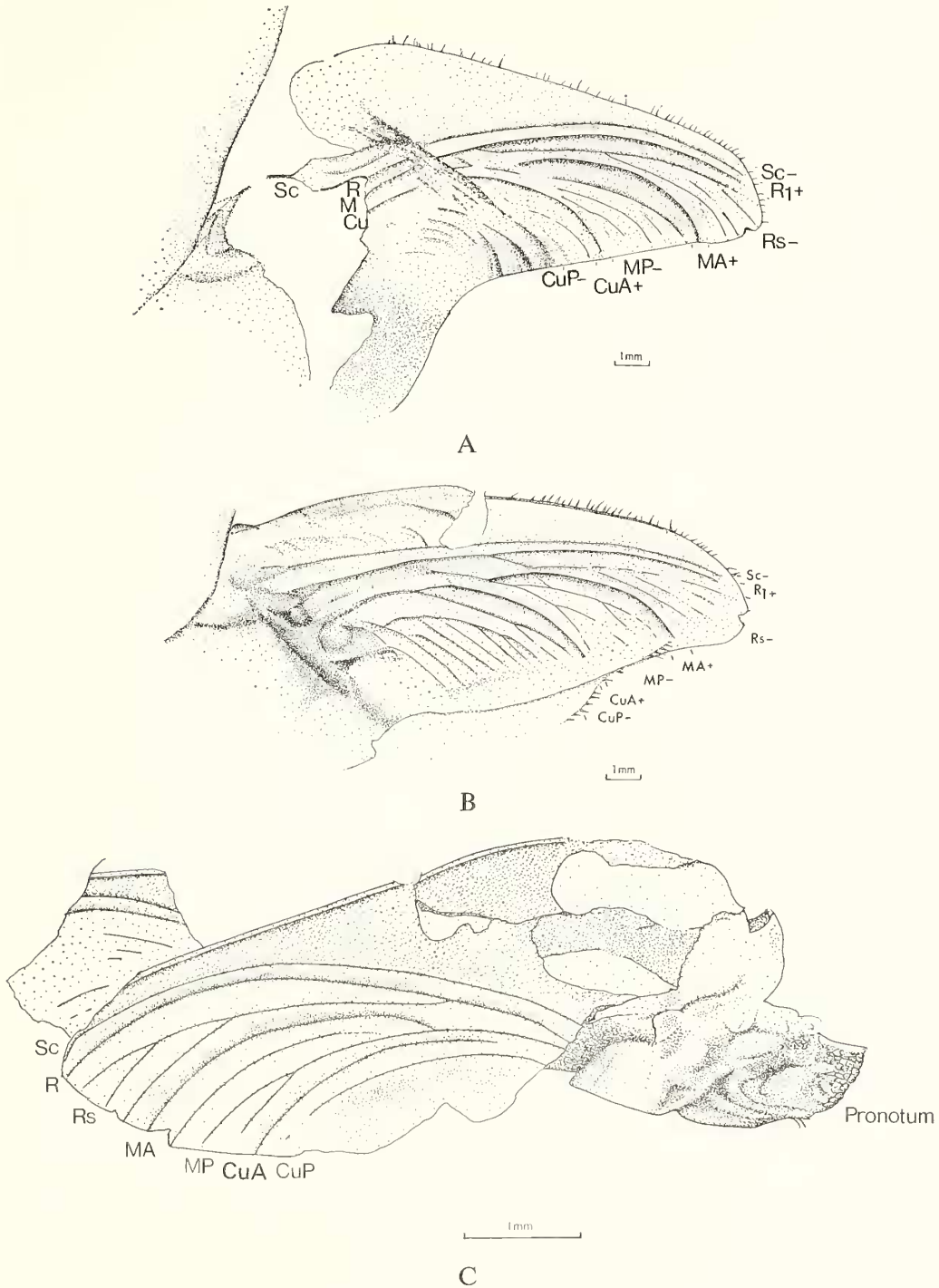
The wing pads are equal in length, but differ in breadth and proportion. Both show the venation in some detail.

Fore wing pad. Length: 15 mm; breadth at base: 8 mm, at halfway: 5 mm. Distance from Sc to hind margin at one-third the wing length from base: 4.5 mm. The anterior part of the pad-base is missing, and the pad is distorted by a transverse crease at about one-quarter its length from the base. Costal field broad and triangular, the basal third of the anterior margin lying perpendicular to the body axis, the remainder at 20°. The posterior margin of the pad is straight, at *c.* 50° to the body axis. Neither precostal strip nor postcostal vein is visible, although their absence cannot be assumed. Sc concave, long, unbranched, curving in the distal part of the pad to run parallel to the anterior margin almost to the wing-tip. R markedly convex, unbranched, nearly parallel to Sc throughout its length. Rs departing from R at about half the pad-length from the base, concave, faintly preserved; probably pectinately 4-branched, although it is possible that the fourth branch forks again distally. MA and MP separate just distally to the divergence-point of R and Rs. MA markedly convex, strongly arched, unbranched. MP concave, faint, five-branched; dividing initially into 3, with the first and third branches dividing again. CuA convex, strongly arched, unbranched. CuP concave, faint, branching obscured. Anal veins obscure.

Hind wing pad. Length: 15 mm; breadth at base: 7.5 mm, at half-way: 6 mm. Distance from Sc to hind margin at one-third the wing-length from base: 5.5 mm. Anterior margin curved, the proximal half appearing slightly arched to form a long low anterior lobe. Costal field much narrower than that of fore wing pad. Precostal strip doubtfully present: an anterior band is visible in the basal half of the wing, but its posterior edge is faint and concave, which is not in keeping with the costa. No postcostal vein visible, but its absence cannot be assumed. Sc long, unbranched, as fore wing. R markedly convex, unbranched, parallel to Sc. Rs departing from R slightly more distally than in fore wing, concave, faint, branching probably as in fore wing. Base of M very faint, apparently concave. MA markedly convex, strongly arched, unbranched. MP concave, faint, branching obscure but probably as fore wing. Cu basally convex; CuA and CuP separating at about one-third the wing-length from the base. CuA strongly convex, unbranched. CuP concave, two-branched. Anal veins pectinately 7-branched; the 6th forking to make 8 branches in all.

At the base of the pad is a line of raised areas which appear to be associated with the longitudinal veins. These may be the precursors of the axillary plates of the wing; and they correspond fairly closely with the pattern described by Kukalová (1960) in *Ostrava nigra*, although the sub-costal plate seems less closely associated with the radial than in that species, and the anal veins appear to arise from a broad raised area associated with the cubital plate, rather than from the plate itself.

Abdomen: tapering towards the rear, with traces of nine abdominal terga; the last four being progressively incomplete and poorly preserved. The posterior margin of each segment is concave. Segment 1 is laterally obscured by the metathoracic wing pad, although a trace of the posterior margin may be seen underlapping the pad. Each remaining segment bears a pointed posterolaterally directed paranotal lobe, not, as in



TEXT-FIG. 3. A, B, *Idoptilus onisciformis*, wing pads, reversed and drawn by tracing photographs. $\times 5$. A. Fore wing pad. B. Hind wing pad. 3 C. Nymph 3. Manchester Museum W1222, $\times 17$. Drawn with camera lucida.

Rochdalia, noticeably raised above the level of the tergum. Each tergum shows a faint line, which may represent the anterior margin of the tergum succeeding.

Affinity. While less of the body of *Idoptilus onisciformis* is preserved than is the case with *Rochdalia parkeri*, the surface details of the preserved parts are far clearer. In particular the wing pad venation provides good evidence for the assignment of the insect to the Palaeodictyoptera.

The venation of many polyneopterous insects resembles to some extent that of Palaeodictyoptera. Two characters, however, indicate that *Idoptilus* was certainly palaeopterous; and these are probably of general value in distinguishing between Palaeoptera and Polyneoptera. Firstly MA and MP are clearly convex and concave respectively, whereas in most if not all Neoptera the median veins are flat; and secondly CuP and 1A of the hind wing are both strongly curved. In all Polyneoptera with fully developed hind wings these veins are straight or nearly so, being aligned with the necessarily straight vannal fold. Unless, therefore, *Idoptilus* belongs to a primitive and otherwise unknown neopterous order which lacks a vannus, it may be taken to belong to the Palaeoptera. Of known Palaeoptera, the venation most nearly resembles that of two groups of Palaeodictyoptera, which are believed by Kukalová (1969*b*) not to be particularly closely related the one to the other. These are the Breyeriidae, whose members show simpler venation than any of the other three families, Homiopteridae, Lycocercidae and Graphiptilidae with which Kukalová groups them; and the assemblage of families including the Eugereonidae, the Megaptilidae and the Archaemegaptilidae. Were the cross-veins or the area at the base of the costa of the fore wing preserved it would be relatively easy to decide to which of these groups the nymph should be referred. In their absence it is difficult. Dr. Rolfe (1967) correctly quotes my having tentatively compared this nymph, whose photographs he had sent me, with the Breyeriidae. I did not and do not, however, believe there to be any evidence for referring *Rochdalia* to this family.

Idoptilus shares with all these families the following characters:

1. At least the median, cubital and anal veins strongly and evenly curved to the hind margin.
2. Sc, R, MA and CuA unbranched.
3. R separating from Rs and MA from MP at nearly the same level.
4. The anterior product of the first forking of Rs branching pectinately several times. In *Idoptilus* the posterior product of the first forking branches once, as in known Eugereonidae and Breyeriidae. In *Archaemegaptilus kiefferi* and *Megaptilus blanchardi* it branches pectinately 2 and 3 times respectively. The mode of branching of Rs in *Dictyoneurella perfecta* Laurentiaux, placed by Kukalová in the Archaemegaptilidae, is different from that of all others in the group of families.
5. The anal veins are pectinately branched.

The number of branches of Rs, MA and CuP falls within the range observed in all the mentioned families, except that no breyeriid is known with more than 4 branches to MA.

Idoptilus further resembles Breyeriidae in having the hind wing broader than, but similar in length and venation to, the fore wing; and in possessing a marginal fringe of

macrotrichia (which may, however, be only a juvenile character in *Idoptilus*). It differs in having Sc long and distinct from R throughout its length, whereas in Breyeriidae it is relatively short, and ends on R.

The venation of the fore and hind wing pads of *Idoptilus* most closely resembles that of the fore wing of *Dictyoptilus* (F. Eugereonidae). The hind wings of this family, however, differ from the fore wings in being shorter, and in the form of the cubital and anal veins (Carpenter 1964, Kukalová 1969*b*). The fore wings of Megaptilidae and Archaeomegaptilidae were probably similar to the hind wings, but the venation of the latter is less like that of *Idoptilus*; and the same is true of the related families Protagrionidae and Calvertiellidae. The only other family of Palaeodictyoptera whose wing venation is comparably simple is the Dictyoneuridae. In this group, however, MP never has more than 3 branches; and the fore and hind wings are similar in breadth.

The precise position of *Idoptilus* must therefore remain in doubt. The proportions of the wings and spacing of the veins recall the fore wings of Eugereonidae more than Breyeriidae, and it may well be that the insect is closest to the former family, although excluded from it by the form of the hind wing. It should be noted, though, that the pronotum and paranota of *Eugereon boeckingi* Dohrn do not particularly resemble those of *Idoptilus*.

Nymph 3

Text-fig. 3c

Description. The specimen consists of a nearly complete mesothoracic wing pad, the tip of another pad, and part of the notum of a thoracic segment; all situated between the bones of the pelvic girdle of the holotype of *Eugyrinus wildi* (Woodward) W 1222, Manchester Museum, from the Soapstone bed, Mountain Four-feet Mine, Carre Heys, Trawden, near Colne, Lancashire (L. Coal Measures, *lenisulcata* zone). The pads are preserved as a concave impression; but the notum is convex, and its sagittal plane is nearly perpendicular to the plane of the wing pads. The relative position of the wing pads and notum clearly does not reflect that in life. The relief of the notum resembles the pronota rather than the mesonota of *Rochdalia* and *Idoptilus*, and it is probably the pronotum of the insect.

The more fragmentary wing pad is poorly preserved, and its venation appears similar to the more complete one. The latter is 6 mm long and *c.* 2.5 mm wide; slightly smaller than those of *Rochdalia*. Its surface is coarsely punctate, especially in the costal area. The latter is basally very broad, and tapers to the wing tip; the costal margin being strongly arched in the basal third of the wing, and nearly straight for the remaining two thirds. This condition clearly recalls the mesonotal pads of *Rochdalia* and *Idoptilus*. Sc is unbranched, long, and evenly curved to the wing tip. R is unbranched, deeply concave (in this impression) and runs almost parallel with Sc. Rs departs from R near the mid point of the wing, and is pectinately 3-branched. MA departs from MP level with the point of separation of R and Rs, and is unbranched, evenly curved, and deeply concave. MP is pectinately 3-branched. CuA is unbranched and concave. CuP appears unbranched, but may be incomplete. It reaches the hind margin at about 2/3 the wing length from the base, indicating that the anal area was long. No anal veins are preserved.

The left half of the pronotum is preserved, and shows strong relief, which is comparable with that of *Rochdalia* and *Idoptilus*, particularly the former.

Affinity. The venation of the wing pad is remarkably simple. In possessing a long Sc; R, MA and CuA unbranched and evenly curved; Rs and MP with few branches, pectinately arranged; and a long anal area, it recalls the Dictyoneuridae and to a lesser extent the Breyeriidae. All known members of these families, however, have more than three branches to Rs; and indeed, unless further branches were added at subsequent moults, this insect had one of the simplest venation patterns of all Palaeodictyoptera. Comparable simplicity occurs in Carboniferous Megasecoptera and in Carboniferous and Permian Ephemeroptera (cf. the wing pads of *Protoreisma* described by Kukalová (1968) from the L. Permian of Oklahoma and Moravia); but the high costal lobe is typical of neither order, and is, as we have seen, associated in *Rochdalia* and *Idoptilus* with the presence of pronotal paranota, continuing the line of these down the side of the thorax. The evidence supports the assumption that this nymph, like the others, belongs to the Palaeodictyoptera. As such it provides one of the earliest records of the Order.

It is uncertain whether the situation of the fragment in the pelvis of *Eugyrinus* is due to the amphibian having eaten a living or dead nymph, or to chance superimposition of the remains. Watson (1941) suggests that the marine origin of the Soapstone bed may indicate that the insect had been eaten.

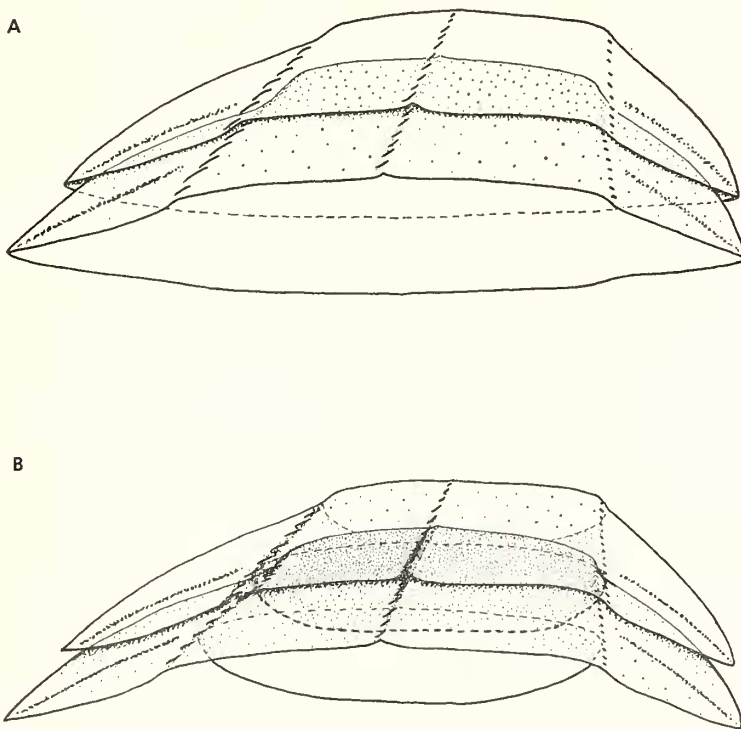
DISCUSSION

The three English palaeodictyopterous nymphs are of interest for the following reasons:

1. While not demonstrably terrestrial, they show no aquatic adaptations.
2. They confirm that the wing pads of juvenile Palaeodictyoptera were postero-laterally directed as in Megasecoptera (Carpenter and Richardson 1968) early Ephemeroptera (Kukalová 1968) and many Neoptera; but unlike those of extant Palaeoptera. This is also apparent from other material, undescribed at the time of writing but mentioned by Carpenter and Richardson (1968, p. 308) and by Sharov (1971).
3. They show that some families, at least, had onisciform nymphs, whose pronotal and abdominal paranota formed with the developing wing pads a series of lateral plates, complete from the head, which they partly shielded, to the end of the abdomen.
4. They show remarkable development of the pronotum, with relief which recalls that of the meso- and metathorax.
5. Their wing pads show precocious development of some adult structures—notably venation (*Idoptilus* and nymph 3) and axillary plates (*Idoptilus*). Moreover both the pads and the pronotal paranota are marked off from the nota by deep furrows, which may have been lines of flexure, and which have also been observed in palaeodictyopterous nymphs from Siberia (Sharov 1971).

The significance of these features requires further investigation, particularly of the thoracic structure of adult forms; but it is beginning to seem possible that these nymphs were capable of moving both wing pads and pronotal paranota, perhaps in association with parachuting and limited gliding (see also Sharov 1971). Smart (1971) has suggested

that the ancestors of Pterygota may have fed on the fruiting bodies of early land plants, but the presence of a muscular clypeal region indicates a liquid feeding habit in Palaeodictyoptera (Carpenter 1971). In either case the selective advantage associated with the development, enlargement and refinement of paranotal lobes could have been increased control of the manner of falling from the food plants, so that the insect tended to reach the ground the right way up. Gliding and direction control would, one imagines, follow.



TEXT-FIG. 4. Diagrammatic representations, from a posterodorsal viewpoint of two pairs of abdominal segments, showing alternative interpretations of the same dorsal view. In A the lateral lobes are the acute posterior angles of the segments; in B they are true paranotal plates.

It may well be that this way of life continued in the nymphs of some early fully-winged insects, and provided reasons for the retention of the pronotal and abdominal paranota.

Many adult Palaeodictyoptera in fact lack abdominal paranota. They have usually been supposed to be present in Dictyoneuridae, but Kukalová (1970) believes that the apparent lateral abdominal expansions in this family are not true paranota but just the strengthened and rather acute posterior angles of the terga.

From a dorsal impression it is not easy to be certain whether a segment fits wholly into the one preceding (text-fig. 4A), and occupies almost all the width of the notum, or whether the notum is extended laterally in paranotal plates (text-fig. 4B). Kukalová (1970) believes the former to be the situation in *Stenodictya*. In *Idoptilus*, and certainly in *Rochdalia*, the latter interpretation is correct, and there can be no doubt that true paranotal lobes are present. The detailed resemblance between the abdominal segments